



**HAL**  
open science

## **Economic costs of invasive alien ants worldwide**

Elena Angulo, Benjamin D. Hoffmann, Liliana Ballesteros-Mejia, Ahmed Taheri, Paride Balzani, Alok Bang, David Renault, Marion Cordonnier, Céline Bellard, Christophe Diagne, et al.

► **To cite this version:**

Elena Angulo, Benjamin D. Hoffmann, Liliana Ballesteros-Mejia, Ahmed Taheri, Paride Balzani, et al.. Economic costs of invasive alien ants worldwide. *Biological Invasions*, 2022, 24 (7), pp.2041-2060. 10.1007/s10530-022-02791-w . hal-03781179

**HAL Id: hal-03781179**

**<https://hal.science/hal-03781179>**

Submitted on 20 Sep 2022

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial - NoDerivatives 4.0 International License



# Economic costs of invasive alien ants worldwide

Elena Angulo · Benjamin D. Hoffmann · Liliana Ballesteros-Mejia · Ahmed Taheri ·  
Paride Balzani · Alok Bang · David Renault · Marion Cordonnier · Céline Bellard ·  
Christophe Diagne · Danish A. Ahmed · Yuya Watari · Franck Courchamp

Received: 18 March 2021 / Accepted: 1 April 2022 / Published online: 25 April 2022  
© The Author(s) 2022

**Abstract** Invasive ants are amongst the most destructive and widespread invaders across the globe; they can strongly alter invaded ecosystems and are responsible for the loss of native ant species. Several studies have reported that invasive ants can also lead to substantial economic costs. In this study, we search, describe and analyse 1342 reported costs of invasive ants compiled in the InvaCost database.

Economic costs, reported since 1930 for 12 ant species in 27 countries, totalled US\$ 51.93 billion, from which US\$ 10.95 billion were incurred, and US\$ 40.98 billion were potential costs (i.e., expected or predicted costs). More than 80% of total costs were associated with only two species, *Solenopsis invicta* and *Wasmannia auropunctata*; and two countries, the USA and Australia. Overall, damage costs amounted to 92% of the total cost, mainly impacting the agriculture, public and social welfare sectors. Management costs were primarily post-invasion management (US\$

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s10530-022-02791-w>.

E. Angulo (✉) · L. Ballesteros-Mejia · M. Cordonnier ·  
C. Bellard · C. Diagne · F. Courchamp  
Université Paris-Saclay, CNRS, AgroParisTech, Ecologie  
Systématique Evolution, 91405 Orsay, France  
e-mail: elenaanguoaguado@gmail.com

*Present Address:*

E. Angulo  
Estación Biológica de Doñana (CSIC), Avda Americo  
Vespucio 26, 41092 Sevilla, Spain

B. D. Hoffmann  
CSIRO, Health & Biosecurity, Tropical Ecosystems  
Research Centre, PMB 44, Winnellie, NT 0822, Australia

A. Taheri  
Département de Biologie, Faculté Des Sciences, Université  
Chouaïb Doukkali, El Jadida, Morocco

P. Balzani  
Department of Biology, University of Florence, Via  
Madonna Del Piano 6, Sesto Fiorentino, 50019 Florence,  
Italy

P. Balzani  
Faculty of Fisheries and Protection of Waters,  
South Bohemian Research Center of Aquaculture  
and Biodiversity of Hydrocenoses, University  
of South Bohemia in České Budějovice, Zátíší 728/II,  
38925 Vodňany, Czech Republic

A. Bang  
Society for Ecology Evolution and Development,  
Wardha 442001, India

D. Renault  
Université de Rennes, CNRS, EcoBio (Ecosystèmes,  
biodiversité, évolution) - UMR 6553, F-35000 Rennes,  
France

D. Renault  
Institut Universitaire de France, 1 rue Descartes,  
75231 Paris Cedex 05, France

1.79 billion), with much lower amounts dedicated to prevention (US\$ 235.63 million). Besides the taxonomic bias, cost information was lacking for an average of 78% of the invaded countries. Moreover, even in countries where costs were reported, such information was available for only 56% of the invaded locations. Our synthesis suggests that the global costs of invasive ants are massive but largely biased towards developed economies, with a huge proportion of underreported costs, and thus most likely grossly underestimated. We advocate for more and improved cost reporting of invasive ants through better collaborations between managers, practitioners and researchers, a crucial basis for adequately informing future budgets and improving proactive management actions of invasive ants.

### Abstract in Spanish - Resumen en español El coste económico mundial de las hormigas invasoras

Las hormigas invasoras están entre las especies más destructivas y más ampliamente extendidas en todo el mundo. Pueden alterar fuertemente los ecosistemas y son responsables de la pérdida de numerosas especies de hormigas nativas en los ecosistemas invadidos. Muchos estudios han mostrado que las hormigas invasoras pueden producir costes económicos importantes. En este estudio, recopilamos, describimos y analizamos 1342 entradas de costes económicos de hormigas invasoras usando la base de datos InvaCost. Los costes económicos fueron reportados desde 1930, para 12 hormigas invasoras, en 27 países, alcanzando un total de \$51.93 mil millones de dólares americanos de los cuales \$10.95 mil millones fueron observados (costes reales) mientras que \$40.98 mil millones de dólares americanos fueron costes potenciales (es decir, costes esperados, no observados). Más del 80% de los costes totales fueron causados por dos especies: *Solenopsis invicta* y *Wasmannia auropunctata*; y en dos países: Estados Unidos y Australia. Los costes debidos a daños alcanzaron el 92% del total,

afectando principalmente a los sectores agrícola y de bienestar social. Los costes de gestión se invirtieron en su mayoría en la gestión de post-invasión (\$1.79 mil millones de dólares), con montos mucho menores de inversión en prevención (\$235.63 millones de dólares). A nivel geográfico, falta información de reportes de costes económicos para aproximadamente un 78% de los países invadidos. Además, incluso en los países donde existían costes reportados, dicha información sólo estaba disponible para el 56% de los lugares invadidos. Nuestra síntesis sugiere que los costes globales de las hormigas invasoras son enormes pero en gran medida sesgados hacia las economías desarrolladas, con una gran proporción de costes sin reportar y por lo tanto gravemente subestimados. Exhortamos entonces, a un mayor y mejor reporte de los costes económicos de las hormigas invasoras a través de una mayor colaboración entre gestores, profesionales e investigadores; lo cual es la base crucial para informar adecuadamente presupuestos futuros y mejorar las actuaciones hacia una gestión proactiva de las hormigas invasoras.

**Keywords** *Anoplolepis* · *Linepithema* · *Wasmannia* · InvaCost · Monetary impacts · Formicidae

### Introduction

Social insects, and particularly ants, are amongst the most impactful invasive alien species (Moller 1996; Holway et al. 2002). Certain biological and ecological characteristics make them particularly strong invaders, e.g., their super-colonial structure, high reproducibility, and strong ability to monopolise environmental resources to outcompete native species (Passera 1994; Holway et al. 2002; Bertelsmeier et al. 2017; Arnan et al. 2018). The small size of ants, their generalist nesting habits and frequent association with environmental/habitat disturbance (Fournier et al. 2019) favour their easy transport by humans, in addition to facilitating their establishment and subsequent spread (Bertelsmeier et al. 2018). Consequently, over 200 ant species have established populations outside their native ranges (Lach et al. 2010; Bertelsmeier et al. 2018). Nineteen of them are recorded in the IUCN list of invasive species (<http://www.iucngisd.org/gisd/>), with five (the Argentine ant, *Linepithema*

D. A. Ahmed

Department of Mathematics and Natural Sciences, Centre for Applied Mathematics and Bioinformatics, Gulf University for Science and Technology, 32093 Hawally, Kuwait

Y. Watari

Forestry and Forest Products Research Institute, 1 Matsunosato, Tsukuba, Ibaraki 305-8687, Japan

*humile*, the red imported fire ant, *Solenopsis invicta*, the African big-headed ant, *Pheidole megacephala*, the little fire ant, *Wasmannia auropunctata*, and the yellow crazy ant, *Anoplolepis gracilipes*) being listed among “100 of the world’s worst invasive alien species” (Lowe et al. 2000). Additionally, about 20 more species have been proposed as potentially invasive or super-invasive (Bertelsmeier et al. 2013; Fournier et al. 2019). It is therefore not surprising that the number of ant species reported as invasive, or exhibiting significant extension in their invaded range, is steadily increasing (e.g., Bertelsmeier et al. 2016; Chifflet et al. 2018; Cordonnier et al. 2020), concomitant with ever-increasing human globalisation and international trade (Bertelsmeier 2021; Seebens et al. 2021).

The consequences of ant invasions are numerous (Holway et al. 2002; Lach and Hooper-Bui 2010). Their negative environmental impacts include the displacement of native ant communities, which scale up to higher trophic levels and affect native vertebrates such as birds, reptiles and amphibians (Allen et al. 2004; Guénard and Dunn 2010; Lach and Hooper-Bui 2010; Alvarez-Blanco et al. 2020, 2021; Bousseyroux et al. 2019). Ant invasions alter ecosystem functions by modifying trophic web dynamics, altering nutrient cycling, or decreasing pollination (e.g., Hansen and Muller 2009; Angulo et al. 2011). Invasive ants also substantially affect human assets (Lard et al. 2002; Motoki et al. 2013), much like invasive insects in general (Bradshaw et al. 2016). Impacts include decreasing agricultural production, infrastructure damage, and human health (Lard et al. 2002; Nelder et al. 2006). For example, the little fire ant has a painful sting and tends to sap-sucking insects, resulting in plantations being completely abandoned (Vanderwoude et al. 2015). Also, the African big-headed ant and the Singapore ant (*Trichomyrmex destructor*) induce substantial economic losses, particularly due to damages to electrical equipment, i.e., they chew through wires which sometimes cause fires (Wetterer 2012). As a result, the economic costs of invasive ant species, including losses and management expenses, are frequently presented as reaching billions of dollars annually. For instance, the estimated total annual cost for the red imported fire ant *S. invicta* was initially estimated at US\$1 billion annually in the US (Pimentel et al. 2005). Other invasive ant species can quickly build large populations and become a

nuisance, as in the case of the yellow crazy ant or the Argentine ant (Holway et al. 2002). Meanwhile, reports on economic costs have been restricted primarily to the evaluation of control costs (Hoffmann et al. 2016).

Despite the significant economic costs associated with ant invasions, such costs have remained poorly reported for most invasive ant species. Most costings rely on those for the red imported fire ant because of its high impacts on health and agriculture, and because it is the most studied invasive ant (Sanders and Suarez 2011; Bertelsmeier et al. 2016). Exacerbating the problem of underreported costs, most published costs have not been based on local economic figures. For example, earlier estimations of costs of red imported fire ant across a variety of economic sectors in Texas (Lard et al. 2002) have been extrapolated both temporally and spatially across the world, to other exotic locations where this invasive ant has already expanded to or potentially could (e.g., Lard et al. 2006; Gutrich et al. 2007; Wylie and Janssen-May 2017; Gruber et al. 2021). More actual quantifications of costs in more locations could increase the visibility of invasive ants, and in turn, ensure that managers, stakeholders and practitioners address the serious concerns they represent more effectively—in particular, the ongoing threat to biodiversity (Diagne et al. 2020). Finally, costings to date are very specific to jurisdictions or commodities and are very fragmented geographically (Hoffmann and Broadhurst 2016). As a result, the holistic picture of the costs of invasive ants is very unclear, and such an analysis has never been attempted before.

The newly developed InvaCost database (Diagne et al. 2020) is the first comprehensive and standardised compilation of economic costs associated with biological invasions worldwide. This database provides unique opportunities to assess and understand the economic impacts of invasions holistically, and has already been used to assess the economic costs associated with specific taxa (e.g., Cuthbert et al. 2021a, b; Haubrock et al. 2021a) and jurisdictions (e.g., Angulo et al. 2021a; Ballesteros-Mejia et al. 2021; Bradshaw et al. 2021; Crystal-Ornelas et al. 2021; Diagne et al. 2021b; Haubrock et al. 2021b; Heringer et al. 2021; Kourantidou et al. 2021; Liu et al. 2021). Here, we took advantage of this newly created database and other reported costs to present the first global assessment of the economic costs of

invasive ants. Our analyses aimed to: (i) determine the ant species associated with reported economic costs; (ii) quantify the type of costs (damage costs vs different types of management costs), as well as their spatial and temporal distributions; (iii) identify the economic sectors impacted by these costs; and (iv) identify the geographic and information gaps for cost reporting.

## Methods

### The InvaCost database

We used the latest version of the InvaCost database (InvaCost\_4.0; 13,123 entries; Diagne et al. 2020, <https://doi.org/10.6084/m9.figshare.12668570>). It contains cost data extracted from documents obtained through standardised literature searches (i.e., using ISI Web of Science platform, Google Scholar and the Google search engine) and targeted searches (i.e., expert consultations to try to fill some of the identified data gaps). One of these targeted searches addressed cost data for invasive ants, specifically focusing on the economic costs of the 19 invasive ant species listed by the IUCN (<http://www.issg.org/database>). Documents with costs were identified using four methods: (i) in the Web of Science platform, we used the same search strings considered by Diagne et al. (2020), but adding the scientific names of the 19 ant species and the economic terms translated in eleven languages (Arabic, Chinese, French, German, Greek, Italian, Japanese, Portuguese, Russian, Spanish, and Ukrainian); (ii) searching for the scientific names of the 19 ant species in the digital database SciELO (Scientific Electronic Library Online) (<https://www.scielo.br>), which catalogues literature mainly originating from South America predominantly written in Spanish or Portuguese; (iii) searching for the scientific names of the 19 ant species in the bibliographic database FORMIS (<http://www.ars.usda.gov/saa/cmave/ifahi/formis>, version 2018 in EndNote X9), which is a composition of several ant literature databases. We used the following economic search items also used by Diagne et al. (2020) “econom\*”, “monetary”, “dollar”, “\$”, “€”, “sterling pound”; (iv) contacting key people (mainly managers and researchers) that we knew of working with invasive ant

management programs for which financial data were either not available or were incomplete.

Using InvaCost, we acknowledge that it has some recognized limitations (Diagne et al. 2020; Diagne et al. 2021a) that might constrain our investigation on the economic costs of invasive ant species. Notably, the data are certainly not exhaustive, given that many sources are either not available in electronic format and/or recorded online, which is for instance likely the case for numerous reports from local structures working on invasion management. Also, we are aware that the ‘dynamic’ nature of this database allows further corrections for potential mistakes currently entered, and on-time adding of novel costs when they are made available. Therefore, all the cost estimates presented here represent ranges that should be viewed in terms of relative orders of magnitude rather than exact figures. Nonetheless, InvaCost is the most current and complete compilation of standardized economic costs of a large set of invaders worldwide, making it the most relevant resource available for our research efforts in this study.

In the InvaCost database, all costs extracted from the sources were converted from local currencies to US\$ to 2017 values (see Diagne et al. 2020 for more specific details). Briefly, cost estimates were first converted from local currencies to US\$, by dividing the cost estimate with the official market exchange rate corresponding to the year of the cost estimation. The cost obtained in US\$ of that year was then converted in 2017 US\$ using an inflation factor (computed by dividing the Consumer Price Index of 2017 by the CPI of the year of the cost estimation) that takes into account the evolution of the value of the US\$ since the year of cost estimation.

From the InvaCost v4.0 database, we extracted data for invasive ant species (selecting the family Formicidae). This process resulted in 701 entries (herein *raw data*, Online Resource 1, tab “Raw\_data”).

### The InvaCost data structure

The *raw data* contained over 60 descriptive cost variables divided into the following groups (Online Resource 1, tab “Descriptors”): (i) the bibliographic information of the documents where the costs were reported, (ii) the area impacted or where the costs were incurred (e.g., spatial scale, location), (iii) the taxonomy of the focal species, (iv) the temporal

extent over which the costs either occurred or were predicted to occur, (v) the typology of each cost reported, and (vi) the economic cost values. We used information mainly from the following four cost descriptors: the type of costs, the type of management, the economic sector impacted by invasive ants, and the nature of implementing the cost value.

The type of costs (column *type\_of\_cost\_merged*) assigned costs to either “damage” costs (most often corresponding to marketed costs, e.g., economic losses due to direct and/or indirect impacts, such as yield loss, medical care, infrastructure damage, or income reduction), or “management” costs (economic resources allocated to actions to avoid the invasion, or to deal with established populations). A third category, “diverse/unspecified”, grouped costs that either could not be separated into the two prior categories or were not specified.

To further scrutinise management actions, data in the “management” category were subdivided in another column (*Management\_type*) as: (i) “pre-invasion management”: monetary investments for preventing establishment in an area (e.g., early detection); (ii) “post-invasion management”: money spent managing established invasive ants in invaded areas (e.g., control, eradication, monitoring); (iii) “knowledge/funding”: money allocated to all actions and operations that could be of interest at all steps of management at pre- and post-invasion stages (e.g., research, information, education); and (iv) a “diverse/unspecified” category for costs that included at least two of the above management categories, when costs included damage and management expenditures simultaneously or when management costs were unspecified.

The impacted economic sectors (column *economic sector*) were: “agriculture” (e.g., yield losses); “authorities-stakeholders” (governmental services and/or organisations such as conservation agencies, forest services that allocate efforts for the management of biological invasions); “health” (costs directly or indirectly related to human medical conditions); and “public and social welfare” (activities, goods or services contributing to human well-being, including local infrastructures such as electrical systems, quality of life such as recreational activities, personal goods such as private properties, public services or market activities). A “diverse/unspecified” category was assigned when costs included at least two categories or were unspecified.

Finally, we also considered the implementation of the costs (column *implementation*). This column classified the cost entries as “observed” if the cost was incurred (e.g., a quantified management cost or damage loss) or “potential” (e.g., predicted crop loss) if the cost was expected or predicted to occur beyond the original spatial and/or temporal observation range. Potential costs could come from two different processes: (a) temporal, to predict future costs: (e.g., control costs during a long-term management action could be predicted or planned); (b) spatial, to predict costs in areas where actual costs do not exist either because there is no data or because the ant has not yet reached the area. Due to these two aspects, potential costs could be higher than observed costs because invasive species have not yet attained a distribution everywhere possible to have an impact, and because there will always be more potential impacts than what is reported.

#### Data screening

Before analysis, the *raw data* were screened to detect and remove all possible errors, duplicates and overlaps to avoid overestimating economic costs. We recorded a justification for all the excluded entries (see columns *removeForAntProject* and *Comments* in Online Resource 1, Tab “Raw\_Data”). Only data classified as highly reliable were kept, with that classification based on the criteria that the cost estimation method was documented, repeatable and/or traceable (column *Reliability*). In addition to the excluded entries described above, four more entries were also excluded as it was not possible to standardise their cost value due to a lack of temporal information about the costs. Therefore, a total of 62 raw cost entries were removed from the analyses.

#### Data processing

In the InvaCost database, the estimation period for a given cost could vary from months to several years. However, in order to be comparable, costs must be annual. We annualised costs covering several years and repeated these annual values over the number of years of each cost occurrence. For example, a cost reporting US\$ 5000 over five years was transformed into five identical costs of US\$ 1000 for each of those years. We used the *expandYearlyCosts* function of the

'invacost' package version 0.3-4 (Leroy et al. 2021) in R version 3.6.3 (R Core Team 2020), which relies on the number of years between the cost entry's starting and ending years given in the corresponding columns of the database. Hence, we obtained comparable annual costs for all cost entries. While the *expand-YearlyCosts* function may have some limitations by (i) assuming that costs occurring in less than one year occurred during a single complete year and (ii) conservatively removing any cost entry that occurred over an unspecified time period, it has the advantage to avoid both overestimations of costs and distribution bias towards certain years (Leroy et al. 2021). The *expanded dataset* resulted in 1341 expanded cost entries (see Online resource 1, tab "Expanded\_data").

### Calculations of economic costs

We calculated temporal trends of the economic impacts of invasive ant species using the function *summarizeCosts* from the *invacost package* version 0.3-4 (Leroy et al. 2021) in R version 3.6.3 (R Core Team 2020). This function calculates average annual costs for the whole study period, providing 10-year average costs based on the annualised cost entries, using the column *ImpactYear* of the *expanded dataset*.

Other calculations were (i) the magnitude of costs for each species and the trend of observed costs entries per species with time; (ii) the percentage of each type of cost (damage and the types of management) and we further split the type of cost with the sectors impacted; (iii) and finally, the percentage of each type of management costs for each species. In these calculations, we split the costs considering the nature of the costs to separate *observed* (incurred) and *potential* costs.

### Geographic gap of the economic costs reported

We quantified the geographic gap in the reporting of costs by relating the number of invaded locations with the number of locations with reported costs for each species in each country. Thus, for each species, we mapped the geographic locations of their costs (reported in the raw database, excluding cost entries marked as "remove"). To obtain geographic coordinates of the costs, the original documents were cross-checked to confirm locations. Locations with various

costs were considered only once, and costs at the country-level were not considered (only *S. invicta* in Australia, China, Japan and the USA, and *L. humile* in Japan had country-level costs).

Occurrence records of the current invasive distribution of each species were obtained from both the GBIF (Global Biodiversity Information Facility, <https://www.gbif.org>) and AntWeb ([www.antweb.org](http://www.antweb.org)). Duplicate geographic coordinates and erroneous coordinates falling outside terrestrial borders were removed.

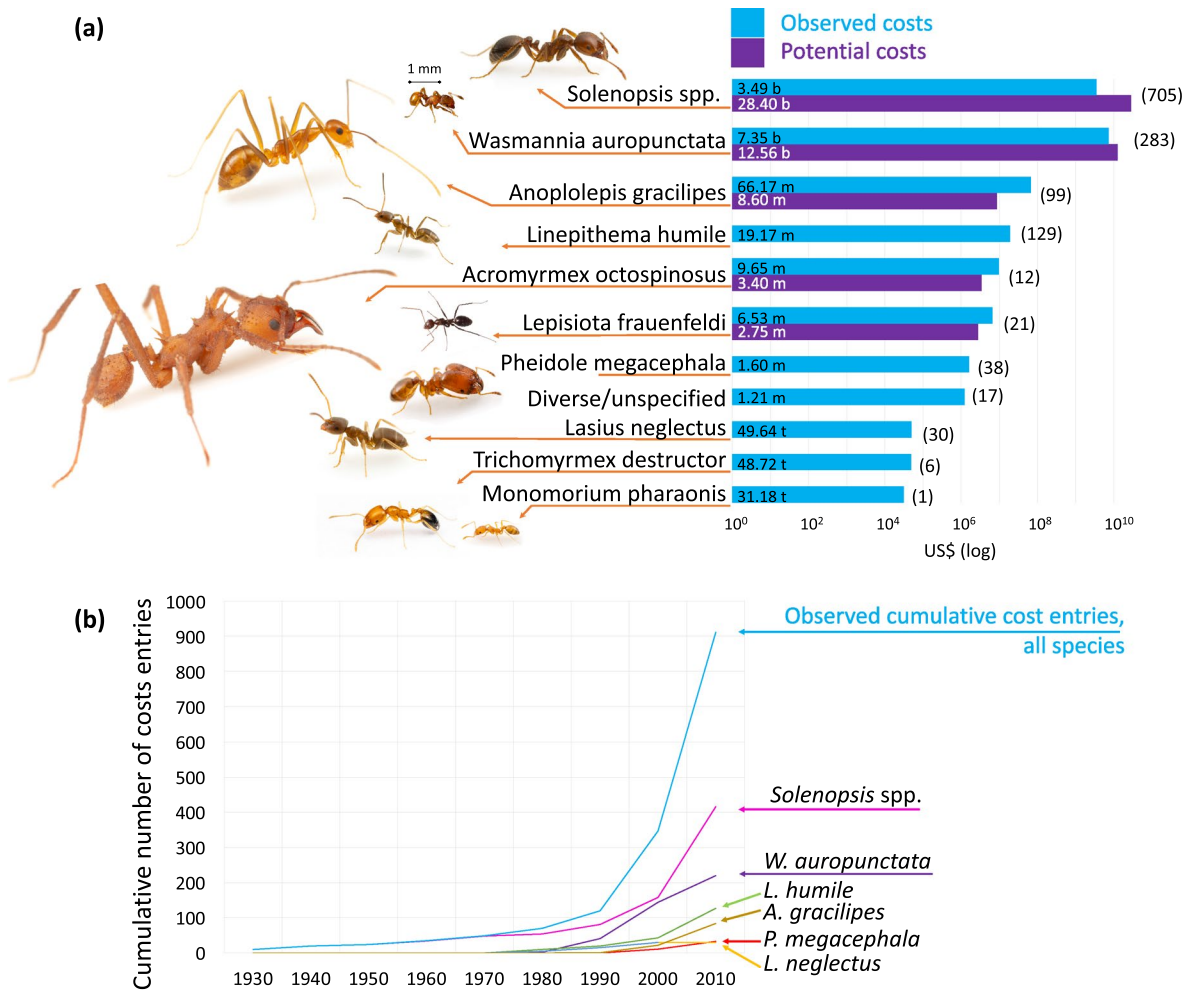
First, for each species, we calculated the percentage of invaded countries without reported costs. Second, for each invaded country with costs incurred by a given species, we calculated the percentage of the number of locations with reported costs in relation to the number of all locations found for the species in that country (ant occurrences). The average of these percentages for all the invaded countries with reported costs for that particular species was referred to as the *geographic coverage* of reported costs for that invasive ant species.

## Results

### Taxonomic distribution of incurred and potential costs in the world

Our dataset contained costs for 12 of the 19 target species, but most of the costs were only for two species, *S. invicta* and *W. auropunctata*.

The largest number of cost entries and highest economic costs were reported for *Solenopsis* spp. (705 expanded cost entries, US\$ 31.89 billion, Fig. 1a, b), followed by *W. auropunctata* (283 expanded cost entries, US\$ 19.91 billion). Although costs were reported for three species of *Solenopsis*, *S. invicta* constituted the most cost entries and economic costs; *S. geminata* was only reported in 8 expanded cost entries for Galápagos Islands (Ecuador) and Ashmore Reef (Australia); the costs for *S. richteri* were reported in the USA, but always together with *S. invicta*. *Solenopsis* spp. were the main drivers, behind the temporal dynamics, of the trends in observed costs, in contrast to the other invasive ant species (Fig. 1b). The number of cost entries (of *Solenopsis* spp. and, to a lesser extent, other ant species) increased with time.



**Fig. 1** Total economic costs reported for invasive ants (US\$, log scale). **a** The total cost per species is expressed in billions (b), millions (m) or thousands (t); the number of cost entries is given in parenthesis; observed and potential costs are separated (upper and lower bars, respectively). **b** Cumulative number of cost entries. Note that, only species with more than 30 cost entries are presented. A 1 mm-scale bar has been added

to show species difference in mean worker body size. Credits for photos of *Solenopsis*, *Anoplolepis*, *Linepithema*, *Acromyrmex*, *Pheidole*, *Lasius* and *Monomorium* correspond to Magdalena Sorger, theantlife.com; for *Trichomyrmex* correspond to Melody Euaparadorn; for *Lepisiota* correspond to The State of Queensland, Department of Agriculture and Fisheries; and for *Wasmannia* correspond to Eli Sarnat

Observed costs were found for all species, but potential costs (expected or predicted) were only reported for five of the twelve species: *Solenopsis invicta*., *W. auropunctata*, *A. gracilipes*, *A. octospinosus* and *L. frauenfeldi* (Fig. 1a). Moreover, potential costs of *Solenopsis* spp. and *W. auropunctata* were higher than observed costs (28.40 versus 3.49 and 12.56 versus 7.35, respectively, in US\$ billion; Fig. 1a), reflecting the large focus of modeling potential impact costs given to these species to justify high expenditure on eradication attempts and

biosecurity. The potential costs for *S. invicta* were mainly related to the expected (planned) costs of the eradication program in Australia (Queensland), and with the spatial extrapolations of damage costs to different locations, e.g., some states in the USA or the Pacific Islands. Most of the potential costs for *W. auropunctata* were extrapolations of damage costs for Hawaii and Vanuatu. Most of the potential costs for *A. octospinosus* were the planned costs of this species' future eradication program in Guadeloupe (Caribbean overseas territory of France). For



*A. gracilipes* and *L. frauenfeldi*, potential costs were for the ongoing eradication programs in Australia.

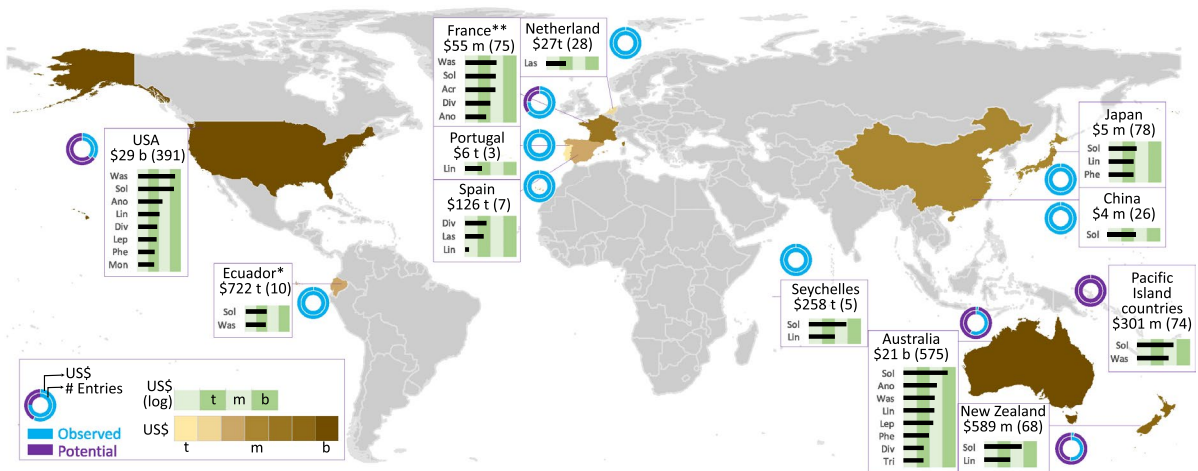
Regarding the distribution of reported costs in the world, most of the economic costs were reported from the USA (391 expanded cost entries, US\$ 29.58 billion) and Australia (575 expanded cost entries, US\$ 21.38 billion) (Fig. 2). Wherever *S. invicta* and *W. auropunctata* occurred in a country, they were associated with the greatest costs incurred, except for Australia, where *A. gracilipes* ranked as the second-costliest (Fig. 2). In most Pacific Island territories, *S. invicta* was the only species with reported costs, all being potential costs because this species is not yet present in the Pacific (Fig. 2, Online Resource 2). In countries such as Seychelles, Portugal, the Netherlands and Spain, where the lowest costs were documented, all losses were observed costs. No costs were reported from many other regions, such as Africa and almost all of South America (except for the Galápagos Islands in Ecuador).

Despite our enhanced search for costs using many languages and even contacting key people directly,

the distribution of the costs in the world was highly biased. From the 1341 cost entries considered, 14% originated from documents written in non-English languages (Japanese, French, Dutch, Chinese, Spanish and Portuguese, listed here by descending number of cost entries), while around 18% were obtained informally from personal communications with managers or researchers.

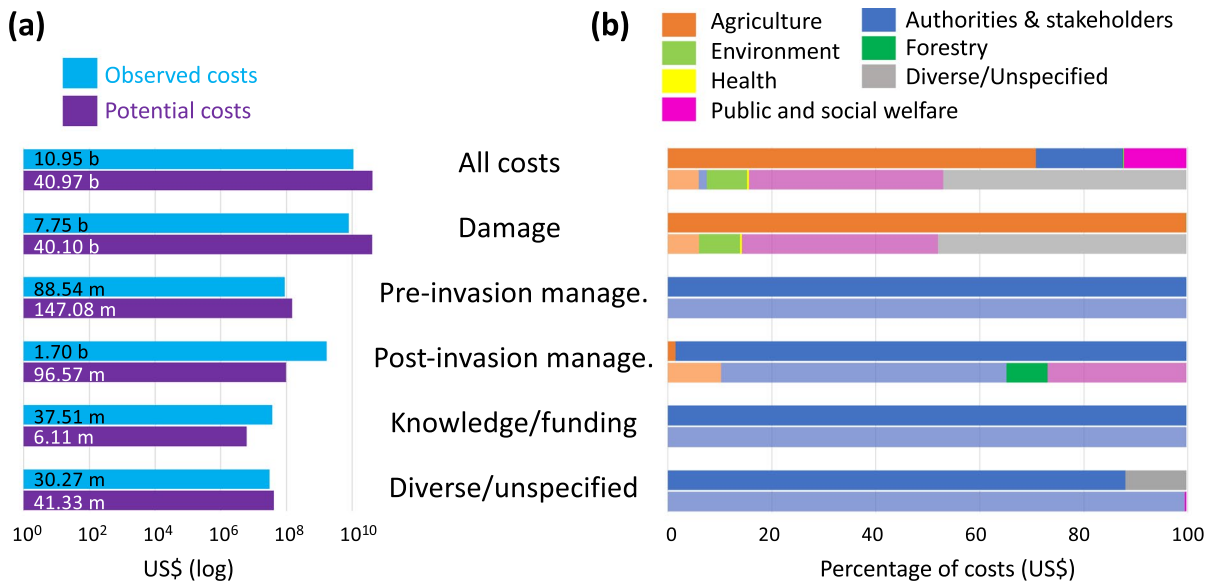
#### Damage loss, management types and economic sectors impacted

Most of the economic costs (92.16%) were categorised as damage costs, of which US\$ 40.10 billion were potential, and US\$ 7.75 billion were actual (Fig. 3a). Management costs amounted to 4.13% of the total costs, with most of the observed management costs assigned to post-invasion management, such as control and eradication (91.56%, US\$ 1.70 billion). In contrast, much lower costs were spent on pre-invasion management actions, such as prevention or early detection (US\$ 88.55 million) and for research activities (US\$ 37.51 million). When



**Fig. 2** Global distribution of costs caused by invasive ant species. The brown colour categorical gradient on the countries reflects the countries with the highest (i.e., dark) to lowest (i.e., light) costs; in the absence of any cost reports, the countries are coloured in grey. Bar graphs on the green scale represent the economic cost per ant species (log scale) in each country. For each country, the total costs (b for billions, m for millions, t for thousands) and the number of cost entries (numbers in parentheses) are added above the bar graph. Circles represent the proportion of observed (blue) and poten-

tial (violet) economic costs (outer circle), and the number of entries (inner circle). \*For Ecuador, all costs are reported for the Galápagos Islands; \*\*for France, all costs are reported for overseas islands; Pacific island countries are grouped. Species codes are: Acr: *Acromyrmex octospinosus*; Ano: *Anoplolepis gracilipes*; Las: *Lasius neglectus*; Lep: *Lepisiota frauenfeldi*; Lin: *Linepithema humile*; Mon: *Monomorium pharaonis*; Phe: *Pheidole megacephala*; Sol: *Solenopsis* spp.; Tri: *Trichomyrmex destructor*; Was: *Wasmannia auropunctata*

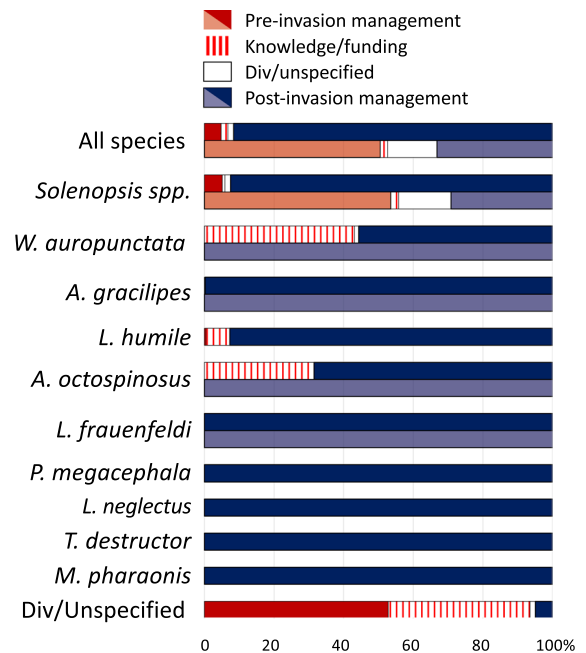


**Fig. 3** Distribution of costs between cost type and associated impacted sectors. For the impacted sector, upper (opaque) bars match observed costs, and lower (semi-transparent) bars match potential costs

focusing on potential costs, future spending on pre-invasion management actions (e.g., avoiding further spread to new areas) is planned to be higher than the amount spent on post-invasion actions (US\$ 147.08 million vs. 96.57 million).

“Agriculture” was the economic sector with the greatest observed costs (70.85%, Fig. 3b). In potential costs, “public and social welfare” was one of the most affected sectors (37.38%). Damage costs strongly drove this general pattern in total costs. Concerning (the much smaller) management costs, the sector with the greatest costs was “authorities and stakeholders” for both potential and observed costs and all types of management (pre-invasion and post-invasion management, “knowledge/funding”, and “diverse/unspecified”). Potential post-invasion costs also impacted other sectors, such as “public and social welfare” (26.9%), agriculture (10.3%) and forestry (7.9%), besides “authorities and stakeholders” (54.86%, Fig. 3b).

Regarding the distribution of the types of management costs for each ant species (Fig. 4), “post-invasion management” was the only type of management cost for most species. Nevertheless, there were some exceptions. For *S. invicta*, potential “pre-invasion management” costs, the ones preventing further spread of an established population, constituted



**Fig. 4** Distribution of management cost types for each ant species. Upper (opaque) bars match observed costs, and lower (semi-transparent) bars match potential costs

a significant part of the total costs (53.57%, Fig. 4). These costs were included in a ten-year eradication plan in Queensland, Australia, although this plan also included post-invasion management actions and “knowledge and funding” actions. For *W. auropunctata* and *A. octospinosus*, the observed cost category “knowledge and funding” was considerable (Fig. 4), constituting 43.12% of total observed costs for *W. auropunctata* spent on general research, and 31.50% for *A. octospinosus*, spent on research for the optimisation of control strategies on Guadeloupe island. The observed pre-invasion management costs for the remaining invasive ants (“Diverse/Unspecified” category) were for biosecurity and the development of educational programs with a focus on invasive ants in New Caledonia (France) (Fig. 4).

#### Geographic gap in the economic costs of invasive ant species

Although most of the costs were only for two species, even for these species, many costs are likely missing because there was no cost reporting in > 80% of the countries they are present (Table 1).

In the case of the countries invaded by *S. invicta*, 51.41% of the locations had reported costs for the three countries with costs (Table 1). However, this percentage was very variable within the three countries (Fig. 5a): there were many ant occurrences in the USA, but few locations with costings. While in Australia, there were more locations with costs reported than where this species occurs, very likely because there have been many eradications, and hence, the species is no longer present in many locations. The third country, China, had intermediate values between the USA and Australia (Fig. 5a). Of the 17 countries that reported costs for *S. invicta*, 14 had no occurrence of the invasive ant. Two of these countries reported observed costs, and the absence of occurrence in the global databases were either because eradication was effective, there are no ant occurrences any more (i.e., New Zealand), or because the cost refers to pre-invasion management (i.e., Japan) (Fig. 5a). In other countries with costs and no occurrences of this invasive ant (Pacific Islands), the costs were potential (extrapolations of damage losses) because *S. invicta* has not yet invaded these islands.

**Table 1** Geographic coverage of reported costs with respect to ant occurrences. For the countries with reported costs, we computed the geographic coverage (percentage of locations with costs with respect to the number of occurrences per species) and provided the number of countries with costs (n). The number of invaded countries without costs and the corresponding percentage is also given. Note that a value higher than 100% for the geographic coverage is possible when there are more locations with costs than occurrences for the species

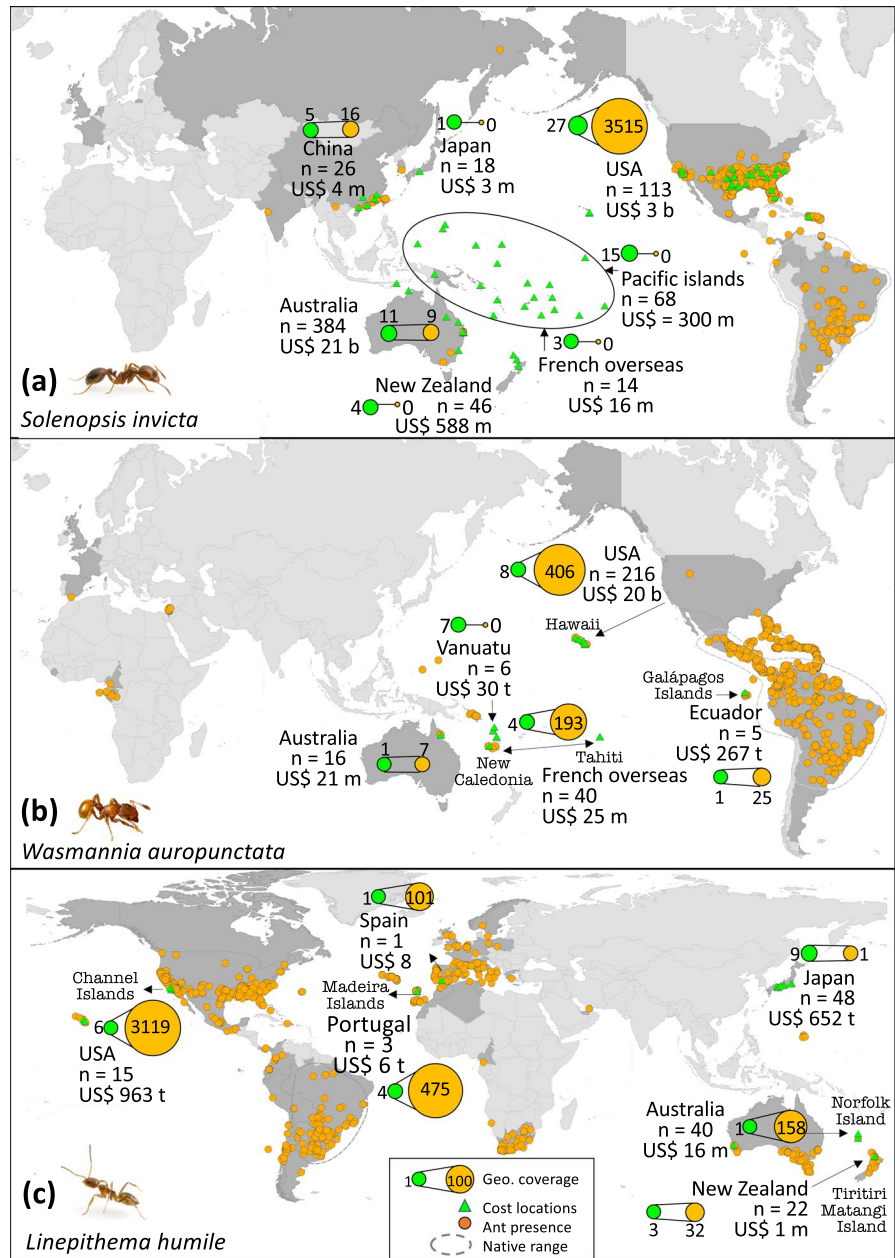
Species	Countries with costs		Countries without costs	
	Geo. coverage	n	%	n
<i>Acromyrmex octospinosus</i>	4.16	1	66.66	2
<i>Anoplolepis gracilipes</i>	3.94	4	80.00	16
<i>Lasius neglectus</i>	81.25	2	85.71	12
<i>Lepisiota frauenfeldi</i>	100	1	66.67	2
<i>Linepithema humile</i>	152.00	6	82.35	28
<i>Monomorium pharaonis</i>	0.43	1	98.55	68
<i>Pheidole megacephala</i>	14.61	4	92.98	53
<i>Solenopsis geminata</i>	108.33	2	93.10	27
<i>Solenopsis invicta</i>	51.41	3	82.35	14
<i>Solenopsis richteri</i>	19.74	1	0.00	0
<i>Trichomyrmex destructor</i>	4	1	97.73	43
<i>Wasmannia auropunctata</i>	7.11	4	88.46	23
<b>Mean</b>	<b>55.88%</b>		<b>77.88%</b>	

For *W. auropunctata*, the mean geographic coverage per country was 7.11%, and by comparing to specific countries, it was the highest in Australia followed by Ecuador and the lowest in France and in the USA (which had the highest numbers of occurrences for this species) (Fig. 5b).

Geographic coverage per country for *L. humile* was > 100%, but costs were reported in only 6 of the 34 invaded countries (Table 1). Cost reporting varied significantly with high reporting in Japan (many costs for very few ant occurrences), and deficient reporting in other countries such as Spain, Portugal, Australia and the USA, where the invasive ant occurs in many locations (Fig. 5c).

For other species, although geographic coverage was variable, the number of countries with reported costs was low, resulting in a mean geographic coverage of reported costs per country for all invasive ants of 55.88% and a mean percentage of invaded countries without costs of 77.88% (Table 1, Online Resource 3).

**Fig. 5** Geographic coverage of economic costs reported for **a** *Solenopsis invicta*, **b** *Wasmannia auropunctata*, and **c** *Linepithema humile*. Countries invaded are marked in dark grey. Orange circles represent ant occurrences, while green triangles represent the locations where costs are reported. For each country, two linked circles represent with their size, the total number of ant occurrences (orange) and the total number of cost locations (green). For illustrative purposes, the maximum circle size is set to 500, so that a higher number of ant occurrences has the same size. The number of cost entries (n), as well as the cost in US\$, is given for each country, in billions (b), millions (m) or thousands (t). In (a), Pacific countries are grouped with an ellipse, together with French overseas territories represented by New Caledonia, French Polynesia, Wallis and Futuna. Only triangles, e.g., in these islands or Japan, means that there are costs but the ant has not yet invaded, has been eradicated or the invasion has not been reported



Final assessment of the costs of invasive ants

The reported cost of invasive ant species amounted to a total of US\$ 51.93 billion, with incurred losses amounting to US\$ 10.95 billion from 1930 to 2021 (reported in 731 entries) and additional potential cost of US\$ 40.98 billion until 2084 (reported in 610 entries). By analysing the temporal distribution of annual costs, the mean annual observed cost

of invasive ants between 1930 and 2021 was US\$ 119.01 million, while the mean annual potential cost between 1982 and 2084 was US\$ 397.84 million. Most of these costs were documented between 2010 and 2019 (Online Resource 4).

## Discussion

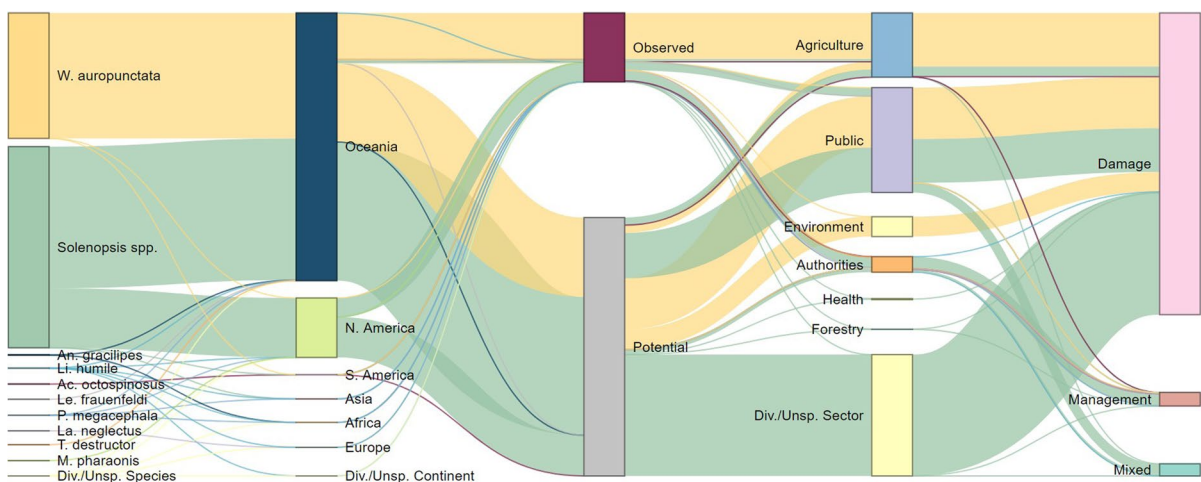
### Alarming economic burden worldwide

Our findings have documented actual costs attributed to ant invasions of at least US\$ 10.95 billion between 1930 and 2020 with additional potential costs of US\$ 40.98 billion (expected and/or predicted to occur in other temporal/spatial scales) from 1980 until 2084. Most reported costs were associated with two invasive ant species, *S. invicta*, the red imported fire ant, and *W. auropunctata*, the little fire ant, which mainly occurred in two countries, the USA and Australia. Most reported costs were associated with damages, particularly impacting the agriculture and public and social welfare sectors (Fig. 6). Management costs constituted only 4.13% of the total amount, the majority of which was spent in post-invasion actions, such as control or eradication. Also, costs were geographically biased: on average, 77.88% of invaded countries per species lacked cost reports, and within invaded countries with costs, the mean geographic coverage of reported costs per species and country was only 55.58%.

Previous research has estimated invasive ants as causing losses and expenditures reaching >US\$ 1 billion annually in specific countries (Pimentel et al. 2005; Gutrich et al. 2007, Wylie and Janssen-May

2017). Our cost compilations show that we lose and/or spend annually US\$ 119 million due to invasive ant species all around the world, increasing by US\$ 398 million annually when including potential costs (i.e., costs planned, expected or predicted to occur). Note that our annual cost compilations are on a global scale for all invasive ant species and over the whole time range of available costs (see Online Resource 1). Notably, for our analyses, cost extrapolations for the USA from Pimentel et al. (2005) were examined and not considered as they overlapped with the estimates provided by Lard et al. (2006). More specifically, both articles used data from Texas (Lard et al. 2002) to extrapolate to other US states, and we considered only Lard et al. (2006) which documented the estimation method used and detailed costs for each activity sector.

Information on economic costs incurred due to invasive ants, both management costs and damage loss, is critically needed as it aids cost–benefit analysis to determine timely management actions (Ahmed et al. 2022). Here, we have shown that incurred costs (costs that have been directly measured) constituted less than 22% of the total costs reported for invasive ants worldwide. Nevertheless, better information on these observed costs can enhance predictive models of the monetary impacts of invasive species under different scenarios, thus providing data-oriented



**Fig. 6** Flow diagram showing the composition of economic costs of invasive ant species among geographical regions, impacted sectors and types of cost. Originating coloured flows correspond to each invasive species. Type of costs comprises

the implementation of the cost (observed vs potential costs) and whether the costs type is management or damage. South America includes countries in Central America; Div./Unsp. corresponds to the category Diverse/Unspecified

suggestions for improved management (Ahmed et al. 2021). In fact, most of the potential costs reported here for invasive ants were extrapolations across both time and space based on observed data. Examples include extrapolations to predict future costs under different management scenarios for *S. invicta* in Queensland (Australia, Hafi et al. 2014), or *W. auro-punctata* in Hawaii (the USA, Motoki et al. 2013), or extrapolations to predict costs (past, present or future costs) in other areas where the same species invade, such as using the costs caused by *Solenopsis spp.* in Texas to predict costs in other invaded states in the USA (Lard et al. 2006; Gutrich et al. 2007) or Australia (Wylie and Janssen-May 2017). Also, all the reported costs for *S. invicta* in the Pacific islands were extrapolated—such areas are expected to be invaded in the future due to their trade history with other areas where ant invasions are prevalent, such as Australia and China (Gruber et al. 2021). While extrapolation is deemed helpful, they are innately highly uncertain; thus, our study highlights the urgent need to provide more observed costs through accurate monitoring and reporting. Moreover, improved cost reporting by managers, practitioners and researchers can raise awareness on the impacts of ant invasions and, in turn, better inform policymakers and enhance public education.

#### A range of impacted sectors

The activity sectors incurring the most damages from invasive ants were mainly agriculture, and public and social welfare. Unfortunately, a large part of the documented costs were not detailed to specific economic sectors in the source information, and thus a high proportion of costs had to be classified as diverse or unspecified.

Costs assigned to the economic sector “Authorities and Stakeholders” (governmental services that allocate efforts for invasive species management) were difficult to categorise, and might have been either overestimated or underestimated, which may affect the actual breakdown of costs across sectors. On the one hand, management by official services that are not specifically linked to another sector were sometimes attributed to this sector, which in turn may inflate costs attributed to this sector, leading to overestimation. On the other hand, underestimation of “Authorities and Stakeholders” costs may have

happened because costs related to government-funded activities were often multisectorial, and thus re-categorized under the sector “Diverse/Unspecified”. We are, thus, aware that costs assigned to this sector could be further refined, as the database is updated over time (Diagne et al. 2020). In our study, this sector was actually associated with most of the observed costs for the management of invasive ants (Fig. 6), i.e., control and eradication programs, mainly done in human settlements or natural areas.

Total costs for agriculture amounted to US\$ 3.61 million for *A. octospinosus* in the French Caribbean, where this ant is known to be a severe pest (Mikheyev 2008; Celini et al. 2012). Reported economic losses in agriculture have also been reported for *W. auro-punctata* in Hawaii (USA), where the nursery and flower exporting sector is expected to be the most affected (Motoki et al. 2013; Vanderwoude et al. 2015). The most detailed costs in the agriculture sector were reported for *S. invicta* where both damage loss and damage repair, as well as control actions, have been quantified, affecting different crops, livestock, farm equipment, or the health of farmers or their animals (Lard et al. 2002, 2006; Gruber et al. 2021). Agricultural impacts of invasive ants could mainly be attributed to the mutualistic relationship of ants with sap-sucking insects, such as aphids and mealybugs, which directly damage the plants and spread plant diseases (Eubanks 2001). Although some benefits to crops from invasive ants have also been reported (for example, *S. invicta* feeding on agricultural pests), the overall influence of invasive ants in the agricultural sector across crop types and interactions is overwhelmingly negative (Lard et al. 2002, 2006). Also, invasive ants can negatively impact livestock production by making it difficult for animals such as chickens to eat or sleep, and through the mortality of newly hatched chicks (Wylie and Janssen-May 2017).

Invasive ants widely affect human infrastructure in different ways and to varying degrees, e.g., destroy electrical equipment, cause damages to property (e.g., cars, TV, telecommunication), resulting in high economic losses (Bradshaw et al. 2016). Costs specifically linked to impacts on human health are also frequently reported in the literature, particularly for those invasive ants that bite humans if disturbed, and whose sting can induce anaphylactic or allergic reactions (Boase 2007). For instance, more than 14 million people are stung annually in the US alone, and

of these, more than 200,000 people require medical treatment (Hoffman 1995). In our data, only one species in one country, i.e., *S. invicta* in the USA, inflicted observed medical costs (Lard et al. 2002). Moreover, potential medical costs were estimated for the Pacific islands, where outdoor activities are frequent, given that ant invasions could occur in such countries in the future (e.g., Gruber et al. 2021). However, damage loss caused by *W. auropunctata*, assigned to the public and social welfare sector, such as reduced property values or lodging in Hawaii (USA), is due to a reduction in recreational activities in outdoor areas, as this sector is not prone to biting and stinging insects (Motoki et al. 2013; Lee et al. 2015). Ant species can also act as pathogen vectors, with some species carrying diseases that can be transmitted to humans, likely causing a wide range of serious infections (Moreira et al. 2005). For instance, several ant species collected in Brazilian hospitals showed associated bacterial growth, e.g., the invasive species *P. megacephala* (Fontana et al. 2010). Economic costs are scarcely available, despite the above implications for health impacts, demonstrating yet another critical knowledge gap that needs urgent attention.

#### Duality of costs: damage vs management

Although the reported economic costs of management were substantially lower compared to the reported cost of damages, the literature shows that the management of invasive ants itself is difficult and can be very expensive (Hoffmann et al. 2010, 2016). However, early responses and other prevention measures implemented to avoid the expansion of early introductions can reduce post-invasion costs and damages, which are, in many cases, much higher (Leung et al. 2002, 2012; Essl et al. 2020; Diagne et al. 2021a). We found that the incurred costs of post-invasion management of invasive ants greatly exceeded the costs spent for pre-invasion management measures (it is notable for *S. invicta* for which US\$ 1.57 billion is already spent in post-invasion management versus US\$ 87.81 million spent in pre-invasion strategies). Clearly, current ant invasions should be managed, and budgeting post-invasion management is necessary; but given the detrimental impacts of invaders as well as the difficulty to eradicate them once they are established, budgets should also prioritise prevention

measures and actions (Faulkner et al. 2020; Cuthbert et al. 2022). Interestingly, when focusing on potential costs, expected or planned pre-invasion management actions were more expensive than post-invasion actions; this could likely be an artefact of the InvaCost definition of “pre-invasion management” including costs associated with preventing further spread of an exotic population in an invaded country, not just the likes of national border security preventing new incursions. Therefore, what some people would generally consider to be post-invasion management costs may be classified as pre-invasion management within InvaCost. For example, it is planned to invest US\$ 147 million for pre-invasion measures to avoid range expansion of *S. invicta* to new areas, while only US\$ 80 million for post-invasion actions. In this case, prevention of human-assisted spread is also linked to surveillance (beyond the borders of the invasion), but also to communication and engagement, and research and development (e.g., of new diagnostic services, Janssen 2017).

Many reports of invasive ant control focus on studies from the USA or Australia (Holway et al. 2002; Sanders and Suarez 2011; Hoffmann et al. 2016), which is in line with higher reported economic costs of invasive ants are found in these regions. Moreover, the spatial coverage of the reported costs of management measures were very similar to the spatial coverage of ant eradication programs reported by Hoffmann et al. (2016), indicating that at least the costs for eradication programs are well reported. Thus, most reports come from eradications, while other management costs are underrepresented. Also, some species for which eradications were described in Hoffmann et al. (2016) had no reported costs (i.e., *Tapinoma melanocephalum*, *Monomorium indicum* or *Myrmecia brevinoda*). For example, in the USA, incurred costs are mainly concerned with the eradication program of *W. auropunctata* in Hawaii (US\$ 10.63 million) and the control strategies in the continent for *S. invicta* (~US\$ 3 billion). Similarly, in Australia, the eradication plan of *S. invicta* in Queensland constituted the majority of observed costs, together with the control and eradication programs of *A. gracilipes* in Queensland, Northern Territory, and Christmas Island (Hoffmann et al. 2016).

Interestingly, costs reported for *L. humile*, which is widely distributed worldwide and causes massive ecological impacts in urban, agricultural and

natural environments (Holway et al. 2002; Sanders and Suarez 2011), were much lower than for *Solenopsis* spp., *W. auropunctata* or *A. gracilipes*, which have a much smaller invasive range (see Fig. 5). We suspect that this is because of the relative impacts of the species. Both fire ant species mainly affect human health and farming because of their powerful stings, and therefore governments want to extirpate these ants very quickly; whereas, the Argentine ant does not sting or even affect humans, and is predominantly an environmental pest. This disparity is particularly notable in Australia and New Zealand, where *L. humile* has been present longer and inhabits a greater area than *S. invicta*. Even in New Zealand, where *L. humile* has been present since the 1990s, a National Invasive Ant Surveillance programme was only initiated after the first detection of *S. invicta* in 2001 (Gunawardana et al. 2013). Additionally, all costs for *L. humile* species were incurred and mainly (~US\$ 4 million) in post-invasion management actions on islands, such as eradication programs on the Channel Islands (USA), Norfolk Island (Australia), Tirititi Matangi Island (New Zealand), or Madeira Islands (Portugal) and also in mainland Japan. Given the global notoriety of this invasive species, it remains unclear why reports have not been produced that estimate its financial implications, given that management programs have been carried out in some continental areas, such as a 34-years program in southern Australia (Hoffmann et al. 2010). Potentially, this species became widespread so long ago that focus has instead been given to the other newly arrived or ‘horizon’ species.

Notably, most of these eradication programs are ongoing, which agrees with the increasing trend in the number of reported cost entries for invasive ants worldwide (Fig. 1b) and with the high amount of potential—expected—costs described before. Accordingly, the cost of these programs may not be available as long as they are ongoing. Most of the costs mentioned were obtained directly from the managers of the eradication programs, proving the fundamental importance of the communication between scientists and practitioners and of combining data from different sources and languages (Angulo et al. 2021b).

### Data gaps and cost underestimation

We only have costs reported for the 12 ant species stated, yet most of the costs (76.93% of the cost entries and 99.83% of the economic amount) are for *S. invicta* and *W. auropunctata*, and costs for the rest of the highly invasive ants are lacking. Lower or non-existent costs for other invasive ant species could be due to them being less destructive, or to significant underreporting. Most certainly, a lot of economic costs are neglected, especially of those invasive ant species that are not yet referenced as invasive in the global lists of invasive species, such as *Tetramorium tsushimae* (Steiner et al. 2006), *Cardiocondyla obscurior* (Heinze et al. 2006), *Plagiolepis alluaudi* (Wetterer 2014), *Formica paralugubris* (Frizzi et al. 2018) among others. Although only 19 invasive ant species are referenced in the IUCN database, Lach and Hooper-Bui (2010) already considered that 147 ant species had successfully established populations outside their native range, and 186 species are registered as introduced in the Antweb “Introduced” project in 2020. Moreover, recent studies identified more than 200 ant species that have established outside of their native range through human-mediated transport (Bertelsmeier et al. 2017), while around ~20 of these species have been identified as potentially invasive based on their life-history traits, i.e., at risk of becoming the subsequent invaders such as *Lepisiota canescens* or *Technomyrmex difficilis* (Bertelsmeier et al. 2013; Fournier et al. 2019).

Some invasive alien species have even identifiable characteristics leading them to be more susceptible to induce economic costs. For instance, the invasive garden ant *L. neglectus*, which has invaded all over Europe from Asia Minor (Espadaler et al. 2007), is an opportunistic species with intensive exploitation of aphids that could cause massive damage to infested greenhouses (Rey and Espadaler 2004). *L. neglectus* ants also have a constant presence within homes, inducing food contamination in catering facilities, and is attracted to electrical installations, light switches, power sockets and electrical security systems, damaging them by their activity (Rey and Espadaler 2004). As a result, this pest species could have an economic impact comparable to the Argentine ant *L. humile*, although the costs reported were much lower given that its geographic expansion is only starting (Espadaler et al. 2007; Ugelvig et al. 2008).



With respect to the geographic coverage of the reported costs, even for the most studied invasive species, many costs are lacking. On average, 78% of the number of invaded countries per species had no reports of costs. Further, when costs were reported in a country, less than 18% of locations on average in those invaded countries had reported costs. Additionally, we only mapped occurrence records readily available with geographic coordinates compiled for each ant species, which excluded many records that would have increased the gap if included. Geographic biases could also have arisen because of the authors targeting key people to obtain new costs, thus resulting in the greater representation of Australia, the USA and France. However, our results also show that our search in other languages and sources increased the number of costs by >30%, including costs reporting from other regions. Besides these taxonomic and geographic gaps, many costs could not be analysed because they were published collectively with other taxa and not only ants. For example, Hequet (2009) presented some costs specifically for *W. auropunctata* in New Caledonia, but other costs linked to population sensitisation to invasive alien species or linked to control of *W. auropunctata* were considered together with rodent and plant control in isolated islands.

There are many other types of costs related to invasive alien ants that are possibly not recorded in InvaCost, or under-recorded, which likely contributes to a gross underestimation of their global economic costs. For example, research grants for scientists studying invasive alien ants are typically not recorded as economic costs and therefore largely absent from the InvaCost database. When asking colleagues worldwide about their research grants on invasive alien ants throughout the last 30 years, we came up with 45 responses providing an estimated US\$ 27,000 average per research article (Online Resource 5). If one considers about 4742 research articles during this period on this topic (with the same keyword search in WoS as described in the Methods, except for the economic components), this suggests that this research grants component alone could be in the order of US\$ 127 million (Online Resource 5). This crude estimation does not account for the actual cost of a research project (typically a fraction of the money received by researchers) nor the researchers' salary (often not included in grants), both of which could significantly increase this estimated amount. This information

underlines the existence of substantial additional costs that are not taken into account in the global estimate we provide in this study, and should be considered an invitation to make publicly available all possible monetary costs related to ant invasions.

The economic impact assessment of invasive ants is a rarely pursued enquiry. In addition to quantifying economic impacts, this study highlights the existing knowledge gaps in the form of limited cost information. Moreover, the bias in (ant) invasion biology towards some species and some countries is a well-established fact in the literature (Pyšek et al. 2008; Bellard et al. 2016; Bertelsmeier et al. 2016), and the InvaCost database is entirely dependent upon such studies. Our study also highlights the multiplicity of the adverse impacts caused by invasive ants. These multiple adverse impacts may differ among species, regions and time-scales. Multiple assessment efforts across spatiotemporal scales and taxonomic units are thus required for improving our understanding of the costs caused by these insects.

In conclusion, we present the most comprehensive assessment of the worldwide economic costs of invasive ants to date. Our description shows that the global costs of invasive ants are massive, yet largely underreported, and as a result are most likely grossly underestimated. We found that the largest economic costs were reported for two species (i.e., *Solenopsis spp.* followed by *W. auropunctata*), although many other ant species are also known to be aggressive invaders on a global scale. The largest costs were predominately sourced from two countries (i.e., the USA followed by Australia), highlighting massive geographic gaps as well. We, therefore, highlight the potential difficulty of obtaining a reliable assessment of the total economic costs incurred by invasive ants and advocate for improved cost reporting from managers, practitioners and researchers. Such efforts will help to understand ant invasion costs at a global scale and, in turn, improve management performance and coordination amongst experts from different countries, which is urgently needed as impending ant invasions are likely to increase worldwide.

**Acknowledgements** We thank the “non-English InvaCost team” that searched the web for the invasive ants with non-English economic terms; as well, we are grateful to all environmental managers, practitioners and researchers who kindly answered our requests for information about the costs

of invasive ants, specifically those managers who provided data that completed and refined previously reported estimates.

**Author's contributions** EA, FC and CD conceived the idea. BH, PB, YW, DR, AB, FC and EA, searched for data to populate InvaCost. EA carried out the analysis with the help of AT, FC, LBM and CD. EA and MC took the lead in writing the original draft, with inputs from all the co-authors. All authors read and approved the final version of the manuscript.

**Funding** Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This research was funded through the 2017–2018 Belmont Forum and BiodivERSa joint call for research proposals, under the BiodivScen ERA-Net COFUND program. The French National Research Agency (ANR-14-CE02-0021) and the BNP-Paribas Foundation Climate Initiative funded the InvaCost project that allowed the construction of the InvaCost database. The work was conducted following a workshop funded by the AXA Research Fund Chair of Invasion Biology and is part of the AlienScenario project funded by BiodivERSa and Belmont-Forum call 2018 on biodiversity scenarios, which also funded CD contract (BMBF/PT DLR 01LC1807C). Funds for EA and LBM came from the AXA Research Fund Chair of Invasion Biology of University Paris Saclay. DA was funded by the Kuwait Foundation for the Advancement of Sciences (KFAS) (Grant number: PR1914SM-01) and the Gulf University for Science and Technology (GUST) internal seed fund (Grant Number: 253536). DR thanks InEE-CNRS who supports the national network 'Biological Invasions' (*Groupement de Recherche InvaBio*, 2014–2022). CB was also funded by her salary as a french public agent.

**Availability of data and material** All data generated and analysed during this study are included in this published article (available in the Online Resource 1).

**Code availability** We used the InvaCost R package (Leroy et al. 2021).

## Declarations

**Conflict of interest** The authors declare that there is no conflict of interest.

**Consent for publication** All authors have read and approved the submitted version of the manuscript.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly

from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>

## References

- Ahmed DA, Hudgins EJ, Cuthbert RN, Haubrock P, Renault D, Bonnaud E, Diagne C, Courchamp F (2021) Modelling the damage costs of invasive alien species. *Biol Invasions*. <https://doi.org/10.1007/s10530-021-02586-5>
- Ahmed DA, Hudgins EJ, Cuthbert RN et al (2022) Managing biological invasions: the cost of inaction. *Biol Invasions*. <https://doi.org/10.1007/s10530-022-02755-0>
- Allen C, Epperson D, Garmestani A (2004) Red imported fire ant impacts on wildlife: a decade of research. *Am mid Nat* 152:88–103. [https://doi.org/10.1674/0003-0031\(2004\)152\[0088:rifaioj\]2.0.co;2](https://doi.org/10.1674/0003-0031(2004)152[0088:rifaioj]2.0.co;2)
- Alvarez-Blanco P, Broggi J, Cerdá X, González-Jarri O, Angulo E (2020) Breeding consequences for a songbird nesting in Argentine ant' invaded land. *Biol Invas* 22:2883–2898. <https://doi.org/10.1007/s10530-020-02297-3>
- Alvarez-Blanco P et al (2021) Effects of the argentine ant venom on terrestrial amphibians. *Conserv Biol* 35:216–226. <https://doi.org/10.1111/cobi.13604>
- Angulo E, Caut S, Cerdá X (2011) Scavenging in mediterranean ecosystems: effect of the invasive argentine ant. *Biol Invas* 13:1183–1194. <https://doi.org/10.1007/s10530-011-9953-6>
- Angulo E, Ballesteros-Mejia L, Novoa A, Duboscq-Carra VG, Diagne C, Courchamp F (2021a) Economic costs of invasive alien species in Spain. *NeoBiota* 67:267–297
- Angulo E, Diagne C, Ballesteros-Mejia L et al (2021b) Non-English languages enrich scientific knowledge: the example of economic costs of biological invasions. *Sci Total Environ*. <https://doi.org/10.1016/j.scitotenv.2020.144441>
- Arnan X et al (2018) Dominance–diversity relationships in ant communities differ with invasion. *Glob Change Biol* 24:4614–4625
- Ballesteros-Mejia L, Angulo E, Diagne C, Cooke B, Nuñez MA, Courchamp F (2021) Economic costs of biological invasions in ecuador: the importance of the galapagos islands. *NeoBiota* 67:375–400
- Bellard C, Jeschke JM (2016) A spatial mismatch between invader impacts and research publications. *Conserv Biol* 30(1):230–232
- Bertelsmeier C (2021) Globalization and the anthropogenic spread of invasive social insects. *Curr Opin Insect Sci* 46:16–23. <https://doi.org/10.1016/j.cois.2021.01.006>
- Bertelsmeier C, Luque GM, Courchamp F (2013) Antprofiler – a database of ecological characteristics of ants. *Myrmecol News* 18:73–76
- Bertelsmeier C, Blight O, Courchamp F (2016) Invasions of ants (hymenoptera: formicidae) in light of global climate change. *Myrmecol News* 22:25–42
- Bertelsmeier C, Ollier S, Liebhold A, Keller L (2017) Recent human history governs global ant invasion dynamics. *Nat Ecol Evol* 1:0184. <https://doi.org/10.1038/s41559-017-0184>

- Bertelsmeier C, Ollier S, Liebhold AM, Brockerhoff EG, Ward D, Keller L (2018) Recurrent bridgehead effects accelerate global alien ant spread. *PNAS* 115:5486–5491. <https://doi.org/10.1073/pnas.1801990115>
- Boase C (2007) The trouble with tramp ants. *Int Pest Control* 49:120–122
- Bousseyroux A, Blanvillain C, Darius T, Vanderwoude C, Beaune D (2019) Ecological impacts of the little fire ant (*Wasmannia auropunctata*) in Tahiti. *Pac Conserv Biol* 25:299–307. <https://doi.org/10.1071/pc18035>
- Bradshaw CJ, Leroy B, Bellard C, Roiz D, Albert C, Fournier A, Courchamp F (2016) Massive yet grossly underestimated global costs of invasive insects. *Nat Commun* 7:1–8. <https://doi.org/10.1038/ncomms12986>
- Bradshaw CJ, Hoskins A, Haubrock P, Cuthbert R, Diagne C, Leroy B, Andrews L, Page B, Cassey P, Hoskins A, Courchamp F (2021) Detailed assessment of the reported economic costs of invasive species in Australia. *NeoBiota* 67:511–550
- Celini L, Roy V, Delabie J, Questel K, Mora P (2012) Présence et origine d'*Acromyrmex octospinosus* (Reich, 1793) à saint-barthélemy, petites antilles (hymenoptera, formicidae, attini). *Bull Soc Entomol France* 117:167–172
- Chifflet L, Guzmán NV, Rey O, Confalonieri VA, Calcaterra LA (2018) Southern expansion of the invasive ant *Wasmannia auropunctata* within its native range and its relation with clonality and human activity. *PLoS ONE* 13:e0206602. <https://doi.org/10.1371/journal.pone.0206602>
- Cordonnier M, Bellec A, Escarguel G, Kaufmann B (2020) Effects of urbanization–climate interactions on range expansion in the invasive European pavement ant. *Bas Appl Ecol* 44:46–54. <https://doi.org/10.1016/j.baae.2020.02.003>
- Crystal-Ornelas R, Hudgins EJ, Cuthbert RN, Haubrock PJ, Fantle-Lepczyk J, Angulo E, Kramer AM, Ballesteros-Mejia L, Leroy B, Leung B, López-López E, Diagne C, Courchamp F (2021) Economic costs of biological invasions within North America. *NeoBiota* 67:485–510
- Cuthbert RN, Pattison Z, Taylor NG, Verbrugge L, Diagne C, Ahmed DA, Leroy B, Angulo E, Briski E, Capinha C, Catford JA, Dalu T, Essl F, Gozlan R, Haubrock PJ, Kouranditou M, Kramer AM, Renault D, Wasserman RJ, Courchamp F (2021) Global economic costs of aquatic invasive alien species. *Sci Total Environ* 775:145238. <https://doi.org/10.1016/j.scitotenv.2021.145238>
- Cuthbert RN, Diagne C, Haubrock PJ, Turbelin AJ, Courchamp F (2021a) Are the “100 of the world’s worst” invasive species also the costliest? *Biol Invasions*. <https://doi.org/10.1007/s10530-021-02568-7>
- Cuthbert RN, Diagne C, Hudgins EJ, et al (2022) Biological invasion costs reveal insufficient proactive management worldwide. *Sci Total Environ* 819:153404. <https://doi.org/10.1016/j.scitotenv.2022.153404>
- Diagne C, Leroy B, Gozlan RE et al (2020) Invacost, a public database of the economic costs of biological invasions worldwide. *Sc Data* 7:1–12. <https://doi.org/10.1038/s41597-020-00586-z>
- Diagne C, Leroy B, Vaissière A-C, Gozlan RE, Roiz D, Jarić I, Salles JM, Bradshaw CJA, Courchamp F (2021a) High and rising economic costs of biological invasions worldwide. *Nature*. <https://doi.org/10.1038/s41586-021-03405-6>
- Diagne C, Turbelin A, Moodley D, Novoa A, Leroy B, Angulo E, Adamjy T, Dia CA, Taheri A, Tambo J, Dobigny G, Courchamp F (2021b) The economic costs of biological invasions in Africa: a growing but neglected threat? *NeoBiota* 67:11–51
- Espadaler X, Tartally A, Schultz R, Seifert B, Cs N (2007) Regional trends and preliminary results on the local expansion rate in the invasive garden ant, *Lasius neglectus* (hymenoptera, formicidae). *Insectes Soc* 54:293–301. <https://doi.org/10.1007/s00040-007-0944-7>
- Essl F et al (2020) The convention on biological diversity (CBD)’s post-2020 target on invasive alien species—what should it include and how should it be monitored? *NeoBiota* 62:99–121. <https://doi.org/10.3897/neobiota.62.53972>
- Eubanks MD (2001) Estimates of the direct and indirect effects of red imported fire ants on biological control in field crops. *Biol Cont* 21:35–43. <https://doi.org/10.1006/bcon.2001.0923>
- Faulkner KT, Robertson MP, Wilson JR (2020) Stronger regional biosecurity is essential to prevent hundreds of harmful biological invasions. *Global Change Biol* 26:2449–2462. <https://doi.org/10.1111/gcb.15006>
- Fontana R et al (2010) Pathogenic bacteria dissemination by ants (hymenoptera: formicidae) in two hospitals in north-east Brazil. *Neotrop Entomol* 39:655–663
- Fournier A, Penone C, Pennino MG, Courchamp F (2019) Predicting future invaders and future invasions. *PNAS* 116:7905–7910. <https://doi.org/10.1073/pnas.1803456116>
- Frizzi F, Masoni A, Quilghini G, Ciampelli P, Santini G (2018) Chronicle of an impact foretold: the fate and effect of the introduced *Formica paralugubris* ant. *Biol Invas* 20:3575–3589. <https://doi.org/10.1007/s10530-018-1797-x>
- Gruber MA, Janssen-May S, Santoro D, Cooling M, Wylie R (2021) Predicting socio-economic and biodiversity impacts of invasive species: red imported fire ant in the developing western pacific. *Ecol Manag Restorat* 22:89–99. <https://doi.org/10.1111/emr.12457>
- Guénard B, Dunn RR (2010) A new (old), invasive ant in the hardwood forests of eastern North America and its potentially widespread impacts. *PLoS ONE* 5:e11614. <https://doi.org/10.1371/journal.pone.0011614>
- Gunawardana DN, Peacock LR, Flynn AR, Ashcroft TT, Green OR (2013) Why is napier sea port a hot spot for invasive ants. *N Z Plant Prot* 66:10–16
- Gutrich JJ, VanGelder E, Loope L (2007) Potential economic impact of introduction and spread of the red imported fire ant, *Solenopsis invicta*, in Hawaii. *Environ Sci Policy* 10:685–696. <https://doi.org/10.1016/j.envsci.2007.03.007>
- Hafi A, Spring D, Croft L, Kompas T, Morey K (2014) Cost-effectiveness of biosecurity response options to red imported fire ants in South East Queensland. Australian bureau of agricultural and resource economics and sciences, department of agriculture, Canberra
- Hansen DM, Müller CB (2009) Invasive ants disrupt gecko pollination and seed dispersal of the endangered plant

- Rousseia simplex* in Mauritius. *Biotropica* 41:202–208. <https://doi.org/10.1111/j.1744-7429.2008.00473.x>
- Haubrock PJ, Turbelin AJ, Cuthbert RN, Novoa A, Taylor NG, Angulo E, Ballesteros-Mejia L, Bodley T, Capinha C, Diagne C, Essl F, Golivets M, Kirichenko N, Kourantidou M, Leroy B, Renault D, Verbrugge L, Courchamp F (2021b) Economic costs of invasive alien species across Europe. *NeoBiota* 67:153–190
- Haubrock PJ, Bernery C, Cuthbert RN, Liu C, Kourantidou M, Leroy B, Turbelin AJ, Kramer AM, Verbrugge LNH, Diagne C, Courchamp F, Gozlan RE (2022a) Knowledge gaps in economic costs of invasive alien fish worldwide. *Sci Total Environ* 803:149875. <https://doi.org/10.1016/j.scitotenv.2021.149875>
- Heinze J, Cremer S, Eckl N, Schrempf A (2006) Stealthy invaders: the biology of cardiocondyla tramp ants. *Insectes Soc* 53:1–7
- Hequet V (2009) Propositions pour la mise en place d'une cellule de veille et de détection précoce des espèces envahissantes en Nouvelle-Calédonie. IRD/AMAP
- Heringer G, Angulo E, Ballesteros-Mejia L, Capinha C, Courchamp F, Diagne C, Duboscq-Carra V, Nuñez M, Zenni RD (2021) The economic costs of biological invasions in Central and South America: a first regional assessment. *NeoBiota* 67:401–426
- Hoffman DR (1995) Fire ant allergy. *Allergy* 50:535–544
- Hoffmann BD, Broadhurst LM (2016) The economic cost of managing invasive species in Australia. *NeoBiota* 31:1–18
- Hoffmann BD, Abbott KL, Davis P (2010) Invasive ant management. *Ant Ecol*. <https://doi.org/10.1007/s00040-005-0847-4>
- Hoffmann BD, Luque GM, Bellard C, Holmes ND, Donlan CJ (2016) Improving invasive ant eradication as a conservation tool: a review. *Biol Conserv* 198:37–49. <https://doi.org/10.1016/j.biocon.2016.03.036>
- Holway DA, Lach L, Suarez AV, Tsutsui ND, Case TJ (2002) The causes and consequences of ant invasions. *Ann Rev Ecol Systemat* 33:181–233. <https://doi.org/10.1093/acprof:oso/9780199544639.003.0015>
- Janssen S (2017) Ten year eradication plan. National red imported fire ant eradication program, South East Queensland, 2017–18 to 2016–27. State of Queensland
- Kourantidou M, Cuthbert RN, Haubrock PJ, Novoa A, Taylor NG, Leroy B, Capinha C, Renault D, Angulo E, Diagne C, Courchamp F (2021) Economic costs of invasive alien species in the mediterranean basin. *NeoBiota* 67:427–458
- Lach L, Linda M, Hooper-Bùi, (2009) Consequences of ant invasions. In: Lach L, Parr C, Abbott K (eds) *Ant ecology*. Oxford university press, pp 261–286. <https://doi.org/10.1093/acprof:oso/9780199544639.003.0015>
- Lard C, Willis DB, Salin V, Robison S (2002) Economic assessments of red imported fire ant on Texas' urban and agricultural sectors. *Southw Entomol* 25:123–137. [https://doi.org/10.1007/springerreference\\_88471](https://doi.org/10.1007/springerreference_88471)
- Lard, CF, Schmidt J, Morris B, Estes L, Ryan C, Bergquist D (2006) An economic impact of imported fire ants in the United States of America. Texas A&M University, Department of Agricultural Economics, Texas Agricultural Experiment Station, College Station, TX
- Lee DJ, Motoki M, Vanderwoude C, Nakamoto ST, Leung P (2015) Taking the sting out of little fire ant in Hawaii. *Ecol Econ* 111:100–110. <https://doi.org/10.1016/j.ecolecon.2015.01.010>
- Leroy B et al (2021) Analysing global economic costs of invasive alien species with the invacost R package. *bioRxiv*. <https://doi.org/10.1101/2020.12.10.419432>
- Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lambert G (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. *PRS Biol Sci* 269:2407–2413. <https://doi.org/10.1098/rspb.2002.2179>
- Leung B et al (2012) TEASing apart alien species risk assessments: a framework for best practices. *Ecol Lett* 15:1475–1493. <https://doi.org/10.1111/ele.12003>
- Liu C, Diagne C, Angulo E, Banerjee A-K, Chen Y, Cuthbert RN, Haubrock PJ, Kirichenko A, Pattinson Z, Watari Y, Xiong W, Courchamp F (2021) Economic costs of biological invasions in Asia. *Neobiota* 67:53–78
- Lowe S, Browne M, Boudjelas S, De Poorter M (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database. *Encycl Biol Invasions*. <https://doi.org/10.1525/9780520948433-159>
- Mikheyev AS (2008) History, genetics and pathology of a leaf-cutting ant introduction: a case study of the guadeloupe invasion. *Biol Invas* 10:467–473. <https://doi.org/10.1007/s10530-007-9144-7>
- Moller H (1996) Lessons for invasion theory from social insects. *Biol Conserv* 78:125–142. [https://doi.org/10.1016/0006-3207\(96\)00022-5](https://doi.org/10.1016/0006-3207(96)00022-5)
- Moreira D, Morais VD, Vieira-da-Motta O, Campos-Farinha AEDC, Tonhasca A Jr (2005) Ants as carriers of antibiotic-resistant bacteria in hospitals. *Neotrop Entomol* 34:999–1006
- Motoki M, Lee DJ, Vanderwoude C, Nakamoto ST, Leung P (2013) A bioeconomic model of Little Fire Ant *Wasmannia auropunctata* in Hawaii. *Pacific Cooperative Studies*, Honolulu
- Nelder MP, Paysen ES, Zungoli PA, Benson EP (2006) Emergence of the introduced ant *Pachycondyla chinensis* (formicidae: ponerinae) as a public health threat in the southeastern United States. *J Med Entomol* 43:1094–1098. [https://doi.org/10.1603/0022-2585\(2006\)43\[1094:eotiap\]2.0.co;2](https://doi.org/10.1603/0022-2585(2006)43[1094:eotiap]2.0.co;2)
- Passera L (1994) Characteristics of tramp species. In: Williams D (ed) *Exotic Ants: biology, impact and control of introduced species*. Westview Press, Boulder, CO, pp 23–43
- Pimentel D, Zuniga R, Morrison D (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecol Econom* 52:273–288. <https://doi.org/10.1201/b10938-21>
- Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. *Trends Ecol Evol* 23(5):237–244
- R Core Team (2020) R: a language and environment for statistical computing. R foundation for statistical computing, Vienna. <https://www.R-project.org/>
- Rey S, Espadaler X (2004) Area-wide management of the invasive garden ant *Lasius neglectus* (Hymenoptera: Formicidae) in Northeast Spain. *J Agric Urban Entomol* 21:99–112
- Sanders NJ, Suarez AV (2011) Elton's insights into the ecology of ant invasions: lessons learned and lessons still to be

- learned. In: Richardson DM (ed) Fifty years of invasion ecology: the legacy of Charles Elton. Wiley-Blackwell, Oxford, UK, pp 237–251
- Seebens H et al (2021) Projecting the continental accumulation of alien species through to 2050. *Glob Change Biol* 27:970–982. <https://doi.org/10.1111/gcb.15333>
- Steiner FM, Schlick-Steiner BC, Trager JC, Moder K, Sanetra M, Christian E, Stauffer C (2006) *Tetramorium tsushimae*, a new invasive ant in North America. *Biol Inv* 8:117–123. <https://doi.org/10.1007/s10530-004-1249-7>
- Ugelvig LV, Drijfhout FP, Kronauer DJC, Boomsma JJ, Pedersen JS, Cremer S (2008) The introduction history of invasive garden ants in Europe: integrating genetic, chemical and behavioural approaches. *BMC Biol* 6:11. <https://doi.org/10.1186/1741-7007-6-11>
- Vanderwoude C, Montgomery M, Forester H, Hensley E, Adachi MK (2015) The history of little fire ant *Wasmannia auropunctata* roger in the Hawaiian Islands: spread, control, and local eradication. *Proc Hawaiian Entomol Soc* 48:39–50
- Wetterer JK (2012) Worldwide spread of the african big-headed ant, *Pheidole megacephala* (hymenoptera: formicidae). *Myrmecol News* 17:51–62
- Wetterer JK (2014) Worldwide spread of alluaud's little yellow ant, *Plagiolepis alluaudi* (hymenoptera: formicidae). *Myrmecol News* 19:53–59
- Wylie FR, Janssen-May S (2017) Red imported fire ant in Australia: what if we lose the war? *Ecol Manag Restorat* 18:32–44

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.